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de Leeuw, Joep J.; Butler, P.J.; Woakes, A.J.; Zegwaard, Fulco

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Author(s): Joep J. de Leeuw, Fulco Zegwaard, Patrick J. Butler and Anthony J. Woakes

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# Body Cooling and Its Energetic Implications for Feeding and Diving of Tufted Ducks

Joep J. de Leeuw<sup>1,2,\*</sup>

Patrick J. Butler<sup>3</sup>

Anthony J. Woakes<sup>3</sup>

Fulco Zegwaard<sup>1,2</sup>

<sup>1</sup>Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; <sup>2</sup>Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Savoyenstrasse 1a, 1160 Vienna, Austria; <sup>3</sup>School of Biological Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom

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## ABSTRACT

Wintering in a temperate climate with low water temperatures is energetically expensive for diving ducks. The energy costs associated with body cooling due to diving and ingesting large amounts of cold food were measured in tufted ducks (*Aythya fuligula*) feeding on zebra mussels (*Dreissena polymorpha*), using implanted heart rate and body temperature transmitters. The effects of diving depth and food ingestion were measured in two sets of experiments: we measured body cooling and energy costs of six tufted ducks diving to different depths in a 6-m-deep indoor tank; the costs for food ingestion and crushing mussel shells were assessed under seminatural winter conditions with the same ducks feeding on mussels in a 1.5-m-deep outdoor pond. Body temperature dropped during feeding bouts and increased gradually during intermittent resting periods. The temperature drop increased linearly with dive duration. The rate of body cooling increased with feeding depth, but it was lower again at depths below 4 m. Half of the increment in energy costs of diving can be attributed to thermoregulatory heat production, of which approximately 50% is generated after diving to warm up the body. The excess costs for ducks feeding on large-sized mussels could be entirely explained by the estimated energy cost necessary to compensate the heat loss following food ingestion, suggesting that the heat produc-

tion from shell crushing substituted for thermoregulation. Recovery from heat loss is probably a major component of the activity budget of wintering diving ducks.

## Introduction

Most endotherms regulate their body temperature within narrow margins to optimize their metabolic functions (Blaxter 1989). Body temperature can be controlled by a variety of physiological, anatomical, and behavioural adaptations (McNab 1980; Blaxter 1989). Nevertheless, fluctuations in body temperature of 1°–3°C around normal resting levels are characteristic of birds, owing to, for example, variation in activity over the diurnal cycle (Prinzinger et al. 1991) or ingestion of food of considerably lower temperature than the body (Wilson and Culik 1991).

Aquatic birds living in cold environments have to maintain a high body temperature against the considerable cooling properties of water. Therefore, maintenance costs are high for birds resting in water, such as diving ducks (Jenssen and Ekker 1989; Jenssen et al. 1989; Bevan and Butler 1992b; De Leeuw 1996), guillemots (Croll and McLaren 1993), and penguins (Kooyman et al. 1976; Stahel and Nicol 1982). Thermal conductance increases while diving (Kooyman et al. 1976; De Vries and van Eerden 1995), and it is questionable whether body temperature can be maintained during diving when the oxygen supply is limited. Bevan and Butler (1992b) reported that body temperature of tufted ducks *Aythya fuligula* decreased after diving in cold water. A drop in body temperature upon diving has also been reported in other diving endotherms, such as penguins (Butler et al. 1995; Handrich et al. 1997), shags (Bevan et al. 1997), muskrats (*Ondatra zibethicus*; MacArthur 1984), and Weddell seals (*Leptonychotes weddelli*; Kooyman et al. 1980). The metabolic cost associated with body cooling in diving animals is poorly known, because an elevation of metabolism for extra thermoregulation may be postponed until after diving and therefore may be difficult to measure (Butler et al. 1995; De Leeuw 1996; Handrich et al. 1997).

The energy cost to compensate heat loss upon ingesting cold food may also contribute considerably to the daily energy expenditure (DEE) of aquatic birds in winter: for example, 6% of DEE in fish-eating great crested grebes (*Podiceps cristatus*; Wiersma et al. 1995), and 13%–20% in mollusc-feeding eiders (*Somateria mollissima*; Nehls 1995) and tufted ducks (De Leeuw 1997). The contribution of other feeding costs to DEE (costs

\*To whom correspondence should be addressed. Present address: Wageningen Agricultural University, Fish Culture and Fisheries Group, P.O. Box 338, 6700 AH Wageningen, The Netherlands; E-mail: joep.deleeuw@alg.wenv.wau.nl.

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for food acquisition, food processing, digestion) is not straightforward, because heat generated by these activities may to some extent compensate the obligatory costs for thermoregulation (Wieser 1989). The amount of heat that can be substituted seems to vary between nil and full substitution, probably depending on the thermoregulatory demands of the animal under study (see, e.g., Kleiber 1961; Pohl and West 1973; Paladino and King 1984; Wilson and Culik 1991; Nehls 1995; Hawkins et al. 1997).

In the small-sized tufted duck (body mass less than 1 kg) feeding on zebra mussels (*Dreissena polymorpha*), the daily energy costs are extremely high, owing to high thermoregulatory costs for living in cold water (De Leeuw 1997). Diving costs increase at lower water temperatures (Bevan and Butler 1992b; De Leeuw 1996), suggesting considerable thermoregulatory costs in addition to hydromechanical costs of overcoming buoyancy and drag while swimming under water (Lovvorn and Jones 1991; Stephenson 1994). To meet their daily energy demands, tufted ducks consume large amounts of mussels (up to three times their body mass per day; De Leeuw 1997). The mussels are ingested whole and the shells are crushed in the muscular gizzard, probably incurring considerable costs for heating up the large cold food mass and for crushing the shells (Nehls 1995).

We studied the impact of diving and food ingestion on maintaining body temperature and the associated energy costs of feeding in tufted ducks under cold winter conditions, when thermoregulatory demands are maximal. We used implanted heart rate and body temperature transmitters, which allow the birds to perform their natural diving behaviour while rapid changes in metabolic rate can be identified. Heart rate has proven to be a good estimate of energy expenditure in diving tufted ducks (Woakes and Butler 1983; Bevan and Butler 1992b; Bevan et al. 1995). Two sets of experiments were carried out: (1) the costs of body cooling and diving in relation to feeding depth were measured in tufted ducks diving in a 6-m-deep indoor tank, and (2) the costs of feeding on mussels (crushing shells and the ingestion of cold food masses) were determined under seminatural conditions in an 1.5-m-deep outdoor pond. In particular, we focus on the relevance of heat substitution and recovery from heat loss for time and energy budgets of tufted ducks.

## Material and Methods

Six tufted ducks (four males and two females with mean body mass of  $606 \pm 42$  g) were implanted with a heart rate and temperature transmitter under halothane anaesthesia. The pulse-interval-modulated radiotransmitter (details in Butler and Woakes [1989]) was positioned in the abdominal cavity with a bipolar electrocardiograph (ECG) electrode under the sternum close to the heart. The temperature sensor was in the body of the transmitter. A detailed description of the surgical

procedures is given in Stephenson et al. (1986). The ECG signal of the transmitter was recorded via a radio receiver and a purpose-built decoder on tape recorder or video recorder for later analysis. The temperature-modulated frequency of the signal was used to determine body temperature in the abdominal cavity (accurate to  $0.05^\circ\text{C}$ ). During the experimental trials, body temperature was monitored every minute. Heart rate was measured instantaneously by counting the number of heartbeats per minute (from acoustic signals of the recorder), or later analyzed from tape recordings, using the Observer event-recording program (Noldus Information Technology, Wageningen, The Netherlands).

Heart rate data were converted to their metabolic equivalents, according to the equation given by Woakes and Butler (1983) and Bevan and Butler (1992b), as derived from tufted ducks swimming at different speeds ( $\text{MR} = 3.942 \times \text{HR} - 3.879$ , where  $\text{MR}$  = metabolic rate [W],  $\text{HR}$  = heart rate [Hz], assuming  $20.1 \text{ J mL}^{-1}$  oxygen), thereby disregarding individual differences. This equation provides good estimates of energy costs for diving tufted ducks (Bevan et al. 1995). The energy costs were expressed as excess costs over resting costs; that is, the estimated energy costs at resting heart rates were subtracted from the total energy costs estimated for the period of elevated metabolism during and after diving (see De Leeuw 1996). Because the excess energy costs do not refer to instantaneous metabolic rates, we used joules per second spent diving (instead of W) as the basic unit. Heart rate of ducks resting on water was determined from the lowest heartbeat frequency over a period of at least 10 min between two series of dives (dive bouts). Excess costs were determined over entire dive bout cycles (i.e., dive bouts plus their subsequent recovery periods; Fig. 1). Recovery duration refers to the time taken for body temperature to return to its pre-dive level. Bout dive duration is the total time spent underwater in a dive bout. During the experiments the ducks could not rest on land in order to simulate conditions in the wild, where tufted ducks float on the water surface while resting.

### Ducks Feeding on Mussels

The ducks were housed in an outdoor pond ( $9.6 \times 4.8$  m, 1.5 m deep) at the University of Groningen, The Netherlands. The ducks were fed zebra mussels for 2 mo before the start of the experiments. Mussels were caught weekly from Lake IJsselmeer at a location frequently used as a feeding site by wild tufted ducks. Water temperature in the pond was  $4.7^\circ\text{--}6.2^\circ\text{C}$ .

Energy costs of feeding on mussels (handling, shell crushing, and heating up the ingested cold food mass) were determined by feeding the ducks mussels with shell lengths between 15 and 20 mm offered at the water surface. These mussels are swallowed singly (De Leeuw and Van Eerden 1992), and food intake could easily be determined by counting the number of mussels ingested. From the frequency distribution on offer

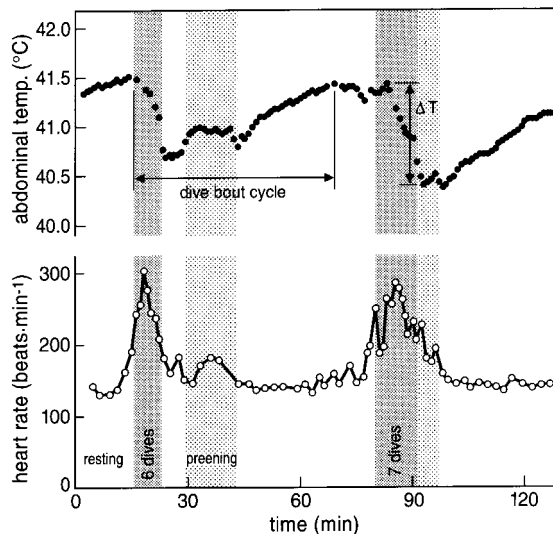


Figure 1. Illustration of changes in heart rate (1-min averages) and abdominal temperature of a tufted duck diving to 5.5 m. Two dive bouts of six and seven dives, respectively, and preening periods are indicated.  $\Delta T$  is the maximum difference in abdominal temperature before and after diving. The unit for energetic measurements was the dive bout cycle (series of dives plus the subsequent period of recovery of temperature drop). Note that the average heart rate is high during diving activity, although it is low during the short submerged periods (see Fig. 5).

and size selection, it was determined that the average mussel ingested weighed 0.8 g (fresh mass, g FM), which is equivalent to 0.56 kJ, as determined from the dry mass of the soft body of mussels and a caloric value of 22.5 kJ g<sup>-1</sup> dry mass (De Leeuw 1997).

Food consumption of mussels at a water depth of 1.5 m was determined from the weight loss of clumps of mussels distributed over a net that was spread over the bottom of the pond. The densities of mussels was low (10–50 g FM m<sup>-2</sup>) and comparable to late winter feeding conditions in the wild

(De Leeuw 1997). Food intake rate was estimated from the weight loss of clumps of mussels recollected in the net (after 50–100 dives were observed) and the total dive duration. These experiments were carried out with two groups of three ducks (two males and one female) per trial to avoid social stress. As diving ducks partly ingest mussels while submerged (De Leeuw and Van Eerden 1992), food intake rates could only be obtained as group averages.

#### *Ducks Diving at Different Depths*

After the mussel-feeding experiments, the same ducks with implanted transmitters were trained for 2 wk to dive in a 6-m-deep tank (diameter 3.9 m) at the Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Vienna (see Carbone et al. [1996] and De Leeuw [1996] for details), where they were fed mealworms and mixed grains. Mealworms were preferred and used during experimental trials to stimulate the ducks to dive to a food tray (1 m × 1 m) positioned at depths between 1.5 and 5.5 m by ropes and pulleys. Five birds (three males and two females) were used in these experiments. The duration of each experimental trial was 2–6 h, and diving depths were 5.5, 1.5, 3.4, 4.5, and 2.5 m, respectively (randomized order). Mean water temperature was 10.2°C (range 7.9–11.5°C) without thermal gradients with depth (the difference between surface temperature and temperature at depth never exceeded 0.5°C).

Two video cameras (one set up at the surface, one in front of a window near the feeding tray) were used to observe the diving behaviour. The images were mixed down onto a single Panasonic video recorder via a digital A/V video mixer and timer (accurate to 0.01 s), while heart rate was recorded via the audio input channel. The behaviour and heartbeat frequencies were later analyzed from video tapes using the Observer event-recording program.

Table 1: Mean (SD) durations of different phases of the dive cycle and recovery after a dive bout averaged for five tufted ducks in relation to diving depth

	Depth (m)				
	1.5	2.5	3.4	4.5	5.5
Descent (s) .....	2.32 (.15)	3.94 (.37)	4.77 (.55)	6.31 (.34)	9.08 (1.26)
Foraging (s) .....	8.09 (2.83)	9.17 (2.47)	8.25 (2.03)	8.75 (1.38)	12.04 (1.18)
Ascent (s) .....	2.32 (.19)	3.29 (.48)	4.01 (.48)	5.47 (.93)	5.34 (.19)
Surface (s) .....	11.6 (3.5)	19.8 (5.2)	20.6 (5.5)	19.6 (3.6)	26.5 (6.4)
Dive (s) .....	12.7 (3.3)	16.4 (2.2)	17.0 (1.6)	20.5 (.4)	26.5 (1.9)
Dives per bout .....	6.9 (2.9)	5.8 (2.7)	3.4 (1.9)	5.2 (1.9)	8.4 (4.1)
Recovery (min) .....	24.6 (10.7)	39.0 (6.0)	20.9 (11.1)	47.3 (15.4)	41.4 (6.3)

Note. Recovery is the time after the last dive in a bout until the abdominal temperature reached the pre-dive level. Water temperature was 10°C.

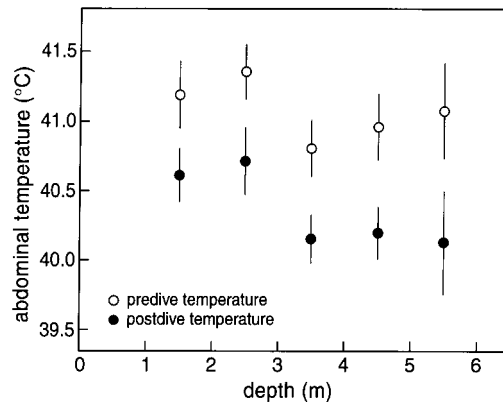


Figure 2. Average maximum and minimum abdominal temperatures (mean and SD) before and after diving, respectively, at different feeding depths in the indoor diving tank. Water temperature was approximately 10°C.

## Results

### Diving-Depth Experiments

**Diving Behaviour.** Diving was confined to short feeding bouts of a series of two to 14 dives with long resting periods (mean = 32 min, SD = 16 min, maximum = 65 min) between dive bouts (example in Fig. 1). After diving the birds were preening or bathing (typically 5–6 min), followed by resting periods, usually with one leg and/or the bill tucked in the feathers. Durations of all phases of the dive cycle increased with diving depth (Table 1). Foraging duration, however, exhibited two phases of increase with depth with a dip at about 3–4 m, as has been earlier reported by Carbone et al. (1996). Descent speed to the feeding tray was on average 0.66 m s<sup>-1</sup> and did not vary between depths (linear regression,  $P > 0.05$ ). In contrast, ascent speed increased with diving depth from 0.65 m s<sup>-1</sup> at 1.5 m to 1.0 m s<sup>-1</sup> at a diving depth of 5.5 m (linear regression,  $r^2 = 0.32$ ,  $P = 0.005$ ). These values are in good agreement with earlier reported values of tufted ducks diving under equivalent conditions (Carbone et al. 1996), suggesting that there was no effect of the implanted transmitters on diving behaviour.

**Abdominal Temperature.** In all trials, the abdominal temperature dropped during a dive bout and subsequently increased gradually (Fig. 1). Highest temperatures were recorded before diving bouts (mean = 41.1°C, SD = 0.5°C,  $N = 26$ ), and lowest temperatures (mean = 40.4°C, SD = 0.5°C) were recorded during preening and resting immediately after diving (Fig. 2). Postdive abdominal temperatures decreased with depth (linear regression  $r^2 = 0.18$ ,  $P = 0.04$ ), suggesting that there is no fixed lower threshold temperature that determines the end of a dive bout under these conditions. The maximum difference in abdominal temperature before and after diving ( $\Delta T$ ) increased with the total time spent underwa-

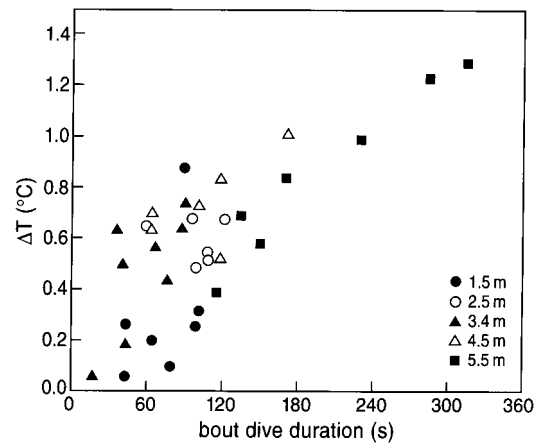


Figure 3. Difference in abdominal temperature before and after diving ( $\Delta T$ ) as a function of total dive duration in a feeding bout at different depths. Water temperature was approximately 10°C.

ter in a dive bout (Fig. 3; linear regression,  $y = 0.0036x + 0.1919$ ,  $r^2 = 0.60$ ,  $P < 0.0001$ ). ANCOVA with bout dive duration and diving depth as covariates and individual as factor revealed that  $\Delta T$  varied with depth and the quadratic term of depth (Depth:  $F_{1, 31} = 11.8$ ,  $P = 0.002$ ; Depth<sup>2</sup>:  $F_{1, 31} = 9.9$ ,  $P = 0.004$ ). The effect of diving depth on cooling rate (°C s<sup>-1</sup> diving) is depicted in Figure 4, indicating that the cooling rate increased with depth up to 3 or 4 m but was lower again at the greatest depths. The recovery period was defined as the duration of abdominal temperature increase after cooling by diving. Recovery duration (10–60 or more min; Table 1) increased with bout dive duration and its quadratic term (stepwise ANCOVA,  $P < 0.05$ , after backward deletion of depth, the square term of depth and individual differences, all  $P > 0.05$ ).

**Heart Rate and Energetics.** Resting heart rate of the five ducks (mean body mass = 608 g, SD = 63) floating on water at 10°C was, on average, 133 beats min<sup>-1</sup> (SD = 8.6; Table 2). Heart

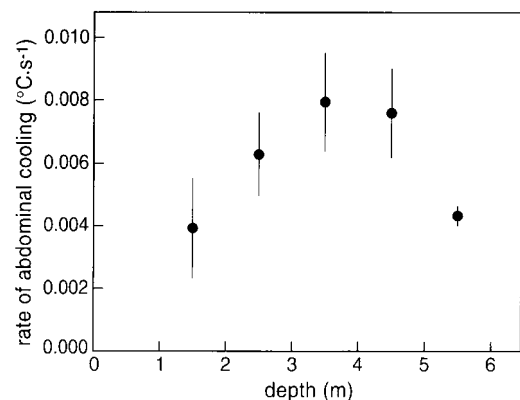


Figure 4. Rate of abdominal cooling (°C drop in temperature per second underwater) in relation to feeding depth.

Table 2: Mean (SD) heart rate (beats min<sup>-1</sup>) at rest in water at 10°C and during different phases of the dive cycle averaged for five tufted ducks in relation to diving depth

	Depth (m)					Mean
	1.5	2.5	3.4	4.5	5.5	
Resting .....	130.0 (9.8)	129.2 (4.1)	145.3 (6.4)	131.2 (8.6)	133.0 (5.6)	132.7 (8.6)
Descent .....	217.9 (29.4)	189.7 (29.1)	211.0 (38.3)	183.0 (44.2)	192.5 (25.6)	198.8 (14.9)
Foraging .....	209.3 (44.1)	194.1 (18.2)	259.2 (73.4)	192.1 (24.5)	194.3 (28.2)	209.8 (28.5)
Ascent .....	220.6 (40.7)	211.1 (27.0)	249.5 (37.1)	192.2 (27.3)	214.9 (19.0)	217.7 (20.7)
Dive .....	211.3 (34.5)	196.5 (18.0)	245.1 (48.0)	190.0 (21.3)	199.2 (21.1)	208.4 (34.8)
Surface .....	241.8 (44.0)	246.6 (48.1)	339.5 (44.1)	264.7 (43.5)	312.1 (29.5)	312.2 (51.2)
Bout .....	224.5 (34.9)	222.6 (34.8)	282.8 (62.1)	230.5 (44.9)	253.9 (26.1)	241.1 (44.1)

Note. Bout refers to the average heart rate during diving and short surfacing intervals of a dive bout.

rate increased before diving and dropped immediately on submergence. Upon surfacing, and slightly anticipating this, heart rate increased to the highest levels recorded, as illustrated in Figure 5. Average heart rate was 208 beats min<sup>-1</sup> (SD = 35) during submergence and 312 beats min<sup>-1</sup> (SD = 51) between dives of a dive bout (Table 2). Heart rates at different phases of the dive cycle were not related to diving depth (ANOVA, all phases  $P > 0.05$ ). Heart rate between dives tended to increase with depth (ANCOVA with depth as covariate and individual as factor;  $P = 0.05$ ). When diving to 3.4 m, heart rates during resting, diving, and surfacing were higher than when diving to other depths (Table 2). It is possible that the higher heart rates observed during both diving and resting in the 3.4-m trials were due to experimental conditions, since heavy rainfall produced abnormal noise on the roof of the experimental room during these trials. Heart rate was highest between dives or immediately after diving during comfort behaviour like bathing, wing flapping, and preening, and gradually decreased to resting levels (Fig. 1).

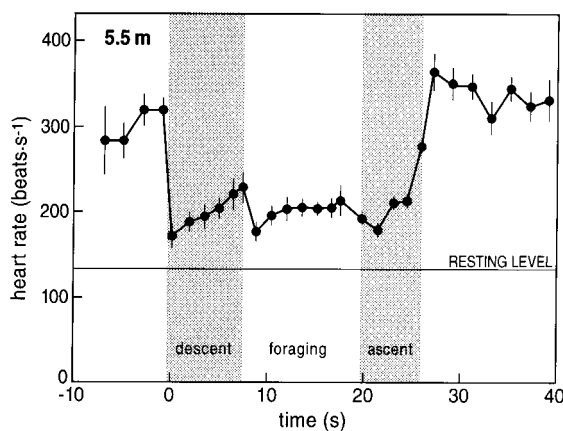


Figure 5. Average heart rate at mean dive duration ( $\pm 1$  s) of tufted ducks diving to 5.5 m ( $N = 12$  dives). Shaded areas indicate travel phases of the dive. Resting heart rate was 130 beats min<sup>-1</sup>.

The estimated excess energy costs (EEC) increased with bout dive duration by 42 J s<sup>-1</sup> diving (Fig. 6; linear regression,  $r^2 = 0.47$ ,  $P = 0.0002$ ,  $y = 42x + 1,175$  J; see Table 3 for correlations between activity, cooling, and EEC). Depth had no significant effect on EEC (ANCOVA with dive duration as covariate:  $F_{4, 19} = 0.85$ ,  $P = 0.51$ ), but individual differences contributed significantly to the variation ( $F_{4, 19} = 4.05$ ,  $P = 0.015$ ; duck 3 > duck 5; see Fig. 6). The mean of the slopes of the regression lines per individual amounts to a comparable estimate for the cost of diving of 38 J s<sup>-1</sup>.

#### Mussel-Feeding Experiments

**Diving and Feeding Behaviour.** The thermal conditions at the outdoor pond were more variable than those at the indoor diving tank, because of wind, snowstorms, and irradiation in the former. In the surface-feeding trials, the amount of mussels

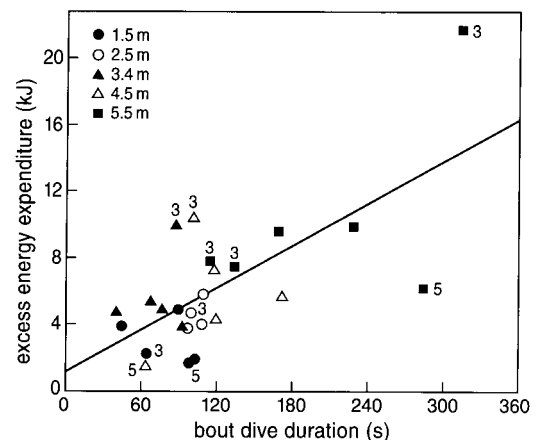


Figure 6. Increase in excess energy expenditure with bout dive duration at different depths. Labelled data refer to ducks 3 and 5, respectively. The slope of the regression line gives the estimate of excess diving costs of 42 J s<sup>-1</sup>.

Table 3: Correlation matrix of energy, time, and temperature parameters in diving depth experiments of tufted ducks

	Depth	Bout Dive Duration	Recovery Duration	Preening Duration	$\Delta T$	EEC
Depth .....	. . .	.454 (.001)	.427 (.033)	.026 (.88)	.352 (.26)	.616 (.001)
Bout dive duration ...	48	. . .	.561 (.004)	.219 (.17)	.773 (<.001)	.686 (<.001)
Recovery duration ....	25	25	. . .	.240 (.35)	.705 (<.001)	.408 (.08)
Preening duration ....	40	40	25	. . .	.193 (.26)	-.023 (.91)
$\Delta T$ .....	40	40	24	36	. . .	.649 (<.001)
EEC .....	25	25	19	25	25	. . .

Note. Upper right cells indicate correlation coefficients, with *P*-values in parentheses; lower left cells indicate number of cases.  $\Delta T$  = abdominal temperature drop after diving; EEC = excess energy cost of diving.

taken per feeding bout (meal size) varied between 1 and 13 g FM (mean = 7.0, SD = 5.0) and meals were separated by short resting intervals of 5.6 min (SD = 3.9), on average. While diving for mussels at a depth of 1.5 m, meal sizes were larger, varying between 3 and 35 g FM (mean = 12.9, SD = 9.3), and the resting periods between feeding bouts were longer (20.0 min; SD = 10.5) than in the surface-feeding trials. Mean dive duration was 13.6 s (SD = 2.4), and the average number of dives in a feeding bout was 8.4 (SD = 4.0). The average crude food intake rate was calculated over complete feeding bouts including resting episodes between bouts. Crude food intake rate was 38 g FM h<sup>-1</sup> during surface-feeding trials and 27 g FM h<sup>-1</sup> in the diving trials.

**Abdominal Temperature.** Both surface-feeding and diving ducks exhibited a drop in abdominal temperature while ingesting food. In the surface-feeding ducks, abdominal cooling amounted to 0.011°C g<sup>-1</sup> mussels ( $y = -0.011x - 0.034$ ,  $r^2 = 0.34$ ,  $P = 0.0001$ ). Abdominal cooling in the diving birds was considerably greater and was weakly correlated with meal size of mussels ( $r^2 = 0.28$ ,  $P = 0.05$ ) or bout dive duration ( $r^2 = 0.30$ ,  $P = 0.04$ ), although in a multiple regression analysis, neither factor was significant ( $P > 0.05$ ).

**Heart Rate and Energetics.** Heart rate during feeding at the surface was on average 154 beats min<sup>-1</sup> (SD = 8.1) or, converted to the rate of energy expenditure, 6.2 W. While diving for mussels, the average heart rate per feeding bout was 227.7 beats min<sup>-1</sup> (SD = 20.4), or 11.1 W. Resting heart rates were on average 121.7 beats min<sup>-1</sup> (SD = 10.1), which amounts to 4.2 W, in both the surface-feeding and diving experiments.

In order to assess the contribution of shell crushing and food heating, the excess energy cost calculated for ducks feeding on mussels at the water surface was compared with the theoretical costs of food heating. These warming-up costs were estimated from the specific heat of mussels (2.8 kJ g<sup>-1</sup> °C<sup>-1</sup>; De Leeuw 1997) and the mussel consumption (g) and the difference in ambient and body temperature. Surface-feeding costs

were only 10% higher than these calculated costs for food heating (Fig. 7) and may partly reflect increased swimming activity while swallowing the mussels. When diving, the costs for feeding on mussels were considerably larger, but not significantly correlated with mussel consumption or bout dive duration ( $P > 0.05$ ).

## Discussion

### Diving Costs

The average metabolic rate estimated from heart rate data during a dive bout (11.4 W) is in good agreement with earlier reported values of approximately 11–14 W obtained by respirometry measurements of diving tufted ducks at similar water temperatures (Woakes and Butler 1983; Bevan and Butler

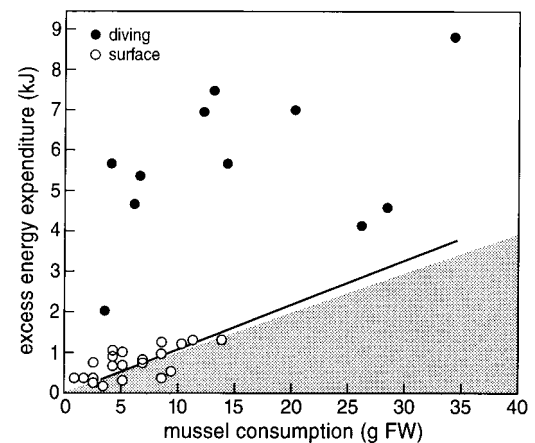


Figure 7. Excess energy expenditure in relation to mussel consumption of tufted ducks feeding at the surface and while diving to 1.5 m in the outdoor pond. The regression line of the surface-feeding costs is similar to the estimated heat compensation for ingesting the cold mussels (shaded boundary). Excess energy expenditure was higher in the diving birds but was not related to mussel consumption.



1992b; De Leeuw 1996). The excess diving costs estimated from heart rate frequencies during and after diving were on average  $42 \text{ J s}^{-1}$  diving. This value is also very similar to the estimate of  $40 \text{ J s}^{-1}$  for excess diving costs reported by De Leeuw (1996) as obtained from oxygen consumption measurements of tufted ducks diving to 2 and 5 m at equivalent water temperatures. In the latter study, excess diving costs increased linearly with lower water temperatures from  $23 \text{ J s}^{-1}$  at  $22^\circ\text{C}$  to  $43 \text{ J s}^{-1}$  at  $8^\circ\text{C}$ , indicating that the thermoregulatory component of diving costs is considerable relative to hydrodynamic costs of diving in cold water. In both studies, the ducks were feeding on mealworms ad lib. The ingestion of mealworms of low temperature contributes slightly to the energy costs. The compensatory heat production for food intake, estimated from the intake rate of mealworms ( $0.04 \text{ g FM s}^{-1}$  diving) and the difference in water temperature ( $10^\circ\text{C}$ ) and body temperature ( $41^\circ\text{C}$ ), amounts to 4 J, assuming a specific heat of  $3.5 \text{ J g}^{-1} ^\circ\text{C}^{-1}$ . By subtraction this would yield a net excess diving cost of  $38 \text{ J s}^{-1}$ .

The observed increase in cooling rate with depth (up to 3–4 m) is consistent with the prediction that the increased water pressure at depth reduces the insulation and, therefore, increases heat loss (Kooyman et al. 1976; Wilson et al. 1992; De Leeuw 1996). It is not clear, however, why this trend did not continue at greater depths. An explanation could be that deeper-diving ducks allow more air in the feathers than ducks diving to shallow depths. This would increase the insulation properties of the plumage, while the hydrodynamic cost of overcoming buoyancy remains low at greater depth, because the volume of air is reduced by the increased water pressure at depth. In support of this hypothesis is the fact that descent speed did not vary with depth, despite the expected decrease in buoyancy at greater depths, but ascent speed, which is determined by the upward buoyant force, strongly increased when returning from greater depths (see Carbone et al. 1996).

In our experiments, the ducks were never in thermal balance in the short term; even when minimal heart rates were recorded between dive bouts, abdominal temperature usually increased slightly. Therefore, the estimated resting metabolic rates ( $4.7 \text{ W}$  in the diving-depth experiments and  $4.2 \text{ W}$  in the mussel-feeding experiments) might have included some recovery costs from heat loss. However, our resting rates obtained from heart rate are significantly lower than the  $5.7 \text{ W}$  reported by Bevan and Butler (1992b) and, for the mussel-feeding birds, lower than the  $4.8 \text{ W}$  found by De Leeuw (1996), values that were obtained from respirometry data at equivalent temperatures. A reason for this slight discrepancy could be that the average oxygen pulse of a heartbeat is larger in thermoregulating resting animals than in active animals. Such a difference in oxygen pulse has been observed in oystercatchers (*Haematopus ostralegus*) resting and walking, at different ambient temperatures (O. Hüppop and M. Kersten, personal communication), and this phenomenon deserves further study. Although our abso-

lute estimates of metabolic rates may be biased, the estimates of excess diving costs from heart rate data (which also include the long periods of resting while body temperature gradually increased) were very similar to respirometry measurements under equivalent conditions. Therefore, we tentatively conclude that possible differences in oxygen pulse did not affect the estimates of excess energy costs in our study.

### Feeding Costs

When the ducks were feeding on mussels offered at the surface, the EEC was very similar to the estimated obligatory cost of thermoregulation to compensate the heat loss from ingesting cold mussels (Fig. 7). This suggests that the energy costs of shell crushing by the gizzard muscles and digestive costs are low and/or that the heat generated by these activities was substituting for the thermoregulatory heat production imposed by ingesting cold food. Several studies are in support of the latter explanation. Nehls (1995) demonstrated that crushing costs in eiders feeding on *Mytilus* shells amount to 75% of the resting metabolic rate in winter and that the costs increase exponentially with shell size. He also showed that approximately 50% of the heat generated for shell crushing could substitute thermoregulatory costs at low ambient temperatures when thermostatic costs were 40% higher than at thermoneutrality. At the high thermoregulatory demands in the present study (more than 100% in excess of basal costs), a larger proportion or all heat may be substituted. Similarly, the heat production from digestion can substitute for thermoregulation, as has been demonstrated in mollusc-feeding eiders (Nehls 1995) and sea otters (*Enhydra lutris*; Costa and Kooyman 1984), guillemots feeding on fish (Hawkins et al. 1997), and muskrats feeding on aquatic vegetation (MacArthur and Campbell 1994). In the latter three studies, the digestive heat was used for thermoregulation while the animals were resting in water at low temperatures. From a consideration of energetic balance, they would otherwise have needed to generate heat by shivering or increasing their activity. Wilson and Culik (1991) demonstrated in Adélie penguins (*Pygoscelis adeliae*) that the elevation in metabolic rate after a meal of cold krill could be fully explained by the need to warm up the ingested meal in the stomach without excess heat generation from digestion.

### Functional Relationship between Cooling and Energy Costs

In periods of high thermoregulatory demand, probably all heat generated by food processing in the core tissues can be used for thermoregulation (Kleiber 1961). It is questionable whether this also holds for heat generated by diving activity. Heat generated during terrestrial locomotion can partly or, at extremely low temperatures, fully substitute for thermoregulatory costs (see, e.g., Pohl and West 1973; Paladino and King 1984; Webster and Weathers 1990; Zerba and Walsberg 1992). During

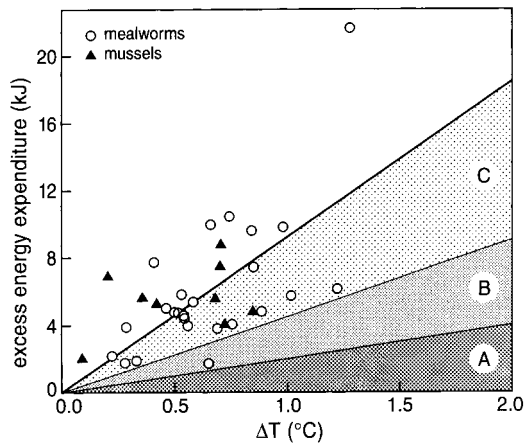


Figure 8. Relationship between excess energy expenditure and the difference in abdominal temperature before and after diving ( $\Delta T$ ). There was no difference in slope between feeding on mussels and feeding on mealworms. The estimated thermoregulatory component of diving (shaded boundary) is composed of the postdive costs of heating up the body after the temperature drop (A) and the ongoing thermoregulatory heat production during diving (B), while the remaining fraction refers to estimated hydrodynamic costs of diving (C).

diving, however, the movement of the hind limbs for locomotion might increase conductive and convective heat loss and the heat generated in the limbs may be difficult to conserve, because blood flow distribution in the peripheral tissues is greatly reduced (Bevan and Butler 1992a). Indeed, excess diving costs depend heavily on water temperature (De Leeuw 1996), indicating that heat generation by activity is insufficient to compensate for heat loss at low water temperatures.

The functional relationship between the extent of body cooling and energy costs of diving is further explored in Figure 8. In our experiments, a temperature drop of  $1^{\circ}\text{C}$  in the abdomen was accompanied by an increase in EEC of 9.1 kJ in all experiments. The contribution of the recovery from a drop in body temperature to EEC can be estimated from the energy cost to increase body temperature of a 600-g tufted duck, assuming a specific heat of  $3.45 \text{ J g}^{-1}$  (Hart 1951). This would amount to  $2.1 \text{ kJ }^{\circ}\text{C}^{-1}$ , under the simplified assumption that the observed cooling in the abdominal cavity would be representative (but probably a maximum) for the whole body. Warming up the whole body would then explain 23% of the excess costs (Fig. 8). This fraction is paid during the preening and resting phase after a dive bout. The remaining costs comprise the hydrodynamic costs of overcoming buoyancy and drag (Lovvorn and Jones 1991; Stephenson 1994) and the elevated thermoregulatory costs during the dive bout (until the end of the drop in body temperature). From the relationship between EEC and water temperature mentioned above (De Leeuw 1996), it can be estimated that the thermoregulatory component attributes about 50% to the diving costs under cold conditions. Since up

to 23% is expended after diving, approximately 27% of the diving costs would be devoted to extra thermoregulation during a dive bout to prevent the body from further cooling. Indeed, the metabolic rate during a dive bout of tufted ducks increases in cold water (Bevan and Butler 1992b; De Leeuw 1996), but the increment is insufficient to maintain a constant body temperature. In king penguins (*Aptenodytes patagonicus*), it has been demonstrated that body cooling is an effective adaptation to extend aerobic diving durations (Handrich et al. 1997).

#### Impact of Body Cooling on Time and Energy Budgets

Crude food intake rate was  $38 \text{ g FM h}^{-1}$  when ducks were feeding on mussels at the surface and  $27 \text{ g FM h}^{-1}$  when diving. To meet the daily energy demands of about 1,800 g FM mussels  $\text{d}^{-1}$  (De Leeuw 1997), the crude food intake rate of tufted ducks must be at least  $75 \text{ g FM h}^{-1}$ . Assuming that intake rate was maximal during feeding bouts, recovery durations between meals should be reduced more than twofold to meet their daily food requirements. In the diving trials, the average drop in abdominal temperature after a meal of 13 g FM amounted to  $0.49^{\circ}\text{C}$ , followed by a recovery period of 20 min on average. In tufted ducks living on mussels in outdoor cages under cold, seminatural conditions, the resting periods between dive bouts were even less than 10 min (De Leeuw 1997). This raises the question whether shorter recovery durations incur higher energy costs. The relationship between recovery time and metabolic heat production was simulated using a Newtonian model of body cooling with compensation by heat production:

$$T_b - T_a = (T_i - T_a)\exp(-tK/C) + (MR/K)[1 - \exp(-tK/C)],$$

where  $T_b$  is body temperature ( $^{\circ}\text{C}$ ) at time  $t$  (s),  $T_a$  is ambient water temperature ( $^{\circ}\text{C}$ ),  $T_i$  is the initial body temperature ( $^{\circ}\text{C}$ ),  $K$  is the dry thermal conductance ( $\text{W }^{\circ}\text{C}^{-1}$ ),  $C$  is the heat capacitance of the animal ( $\text{J }^{\circ}\text{C}^{-1}$ ), assuming a specific heat of  $3.45 \text{ J g}^{-1}$ , and  $MR$  is the metabolic rate (W).  $K$  and  $MR$  were corrected for evaporative heat loss (EHL;  $0.7 \text{ W}$ , as obtained from the evaporative water loss of  $1 \text{ g h}^{-1}$  of tufted ducks at ambient temperatures below  $15^{\circ}\text{C}$  [De Leeuw 1997] and the latent heat of vaporization of water of  $2.427 \text{ kJ g}^{-1}$  [Schmidt-Nielsen 1975]). The thermal conductance was estimated from the metabolic rate of  $5 \text{ W}$  of tufted ducks resting on water (De Leeuw 1996), according to the equation  $K = (MR - \text{EHL})/(T_b - T_a)$ .

This model was used to calculate the (recovery) time for an increase by  $0.5^{\circ}\text{C}$  in temperature of the whole body from an initial temperature of  $40.5^{\circ}\text{C}$  in relation to the metabolic heat production at ambient water temperatures of  $5^{\circ}$  and  $10^{\circ}\text{C}$ ,

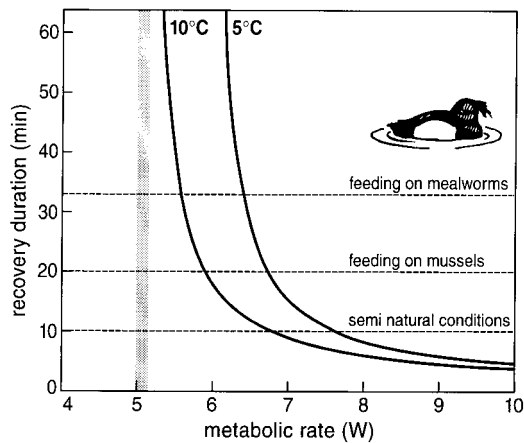


Figure 9. Recovery duration as a function of metabolic rate for a 600-g tufted duck increasing its body temperature of 40.5°C by 0.5°C at a water temperature of 5° and 10°C according to Newtonian cooling with compensation by metabolic heat production (see text). The metabolic rate at thermal balance is 5 W (De Leeuw 1996). The broken lines indicate the observed recovery durations in our indoor experiments and, for comparison, in ducks living on mussels in outdoor, seminatural diving cages (De Leeuw 1997).

respectively (Fig. 9). Figure 9 illustrates that a slight increase in metabolic rate (just above the metabolic rate at thermal balance) can greatly reduce recovery times, but metabolic rate must be considerably higher to recover from a 0.5°C drop in body temperature within 10 min.

Although the model assumes that the total excess cost for increasing body temperature is independent of the metabolic rate (and thus recovery duration), there may be important differences in thermal conductance related to metabolic heat production. During the longer recovery periods, metabolic rate is close to the resting level, and thermal conductance is minimal while the duck is floating quietly on the water surface with the bill and one leg tucked in the feathers. Skin temperatures of eiders floating on cold water were about 30°C, while the core body temperature was 40.4°C, suggesting that peripheral vasoconstriction was used to reduce thermal conductance (Jenssen et al. 1989). However, when resting durations between dive bouts have to be as short as 10 min to meet the daily energy demands, metabolic rate must be increased by 15%, according to the model (Fig. 9). This can probably be realized only by shivering thermogenesis or heat generated by activities like preening (Croll and McLaren 1993; De Leeuw 1996), grooming (MacArthur 1984), or swimming (Costa and Kooyman 1984). Activity, however, might also increase conductance and is therefore less efficient than long resting periods. Wilson and Culik (1991) also argue that endotherms living in cold environments should spread their feeding activity by having long resting periods between meals in order to optimize the use of digestive and activity-generated heat for thermoregulation.

In diving ducks wintering on cold water with energy budgets

close to their metabolic ceiling (Nehls 1995; De Leeuw 1997), we may expect a tendency for long resting durations between meals. During extreme cold spells, diving ducks that are normally active at night extend their feeding activity during the day (see, e.g., Michot et al. 1993; Nilsson 1972; De Leeuw 1997), which may reflect a shift to longer resting periods between meals at night in addition to increased food requirements. However, it may be disadvantageous to spend too much time resting between feeding bouts at the feeding grounds, where the birds may be exposed to strong winds and wave action, which might increase heat loss. Most species of diving ducks do, indeed, prefer to rest during the daytime hours at sheltered areas (Suter 1982; Pedrolí 1982; Burger 1983). From an energetic perspective, resting periods thus seem of great importance in order to balance the energy budget.

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### Literature Cited

- Bevan R.M., I.L. Boyd, P.J. Butler, K. Reid, A.J. Woakes, and J.P. Croxall. 1997. Heart rates and abdominal temperatures of free-ranging South Georgian shags *Phalacrocorax georgianus*. *J. Exp. Biol.* 200:661–675.
- Bevan R.M. and P.J. Butler. 1992a. Cardiac output and blood flow distribution during swimming and voluntary diving of the tufted duck *Aythya fuligula*. *J. Exp. Biol.* 168:199–217.
- . 1992b. The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the tufted duck *Aythya fuligula*. *J. Exp. Biol.* 163:139–151.
- Bevan R.M., J.R. Speakman, and P.J. Butler. 1995. Daily energy expenditure of tufted ducks: a comparison between indirect calorimetry, doubly labelled water and heart rate. *Funct. Ecol.* 9:40–47.
- Blaxter K. 1989. *Energy Metabolism in Animals and Man*. Cambridge University Press, Cambridge.
- Burger J. 1983. Factors affecting distribution of greater scaup *Aythya marila* in a coastal estuary in New York, USA. *Ornis Scand.* 14:309–316.

- Butler P.J., R.M. Bevan, A.J. Woakes, J.P. Croxall, and I.L. Boyd. 1995. The use of data loggers to determine the energetics and physiology of aquatic birds and mammals. *Braz. J. Med. Biol. Res.* 28:1307–1317.
- Butler P.J. and A.J. Woakes. 1989. Telemetry. Pp. 139–170 in C.R. Bridges and P.J. Butler, eds. *Techniques in Comparative Respiratory Physiology: An Experimental Approach*. Cambridge University Press, Cambridge.
- Carbone C., J.J. de Leeuw, and A.I. Houston. 1996. Adjustments in the diving time budgets of tufted duck and pochard: is there evidence for a mix of metabolic pathways? *Anim. Behav.* 51:1257–1268.
- Costa D.P. and G.L. Kooyman. 1984. Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter *Enhydra lutris*. *Physiol. Zool.* 57:199–203.
- Croll D.A. and E. McLaren. 1993. Diving metabolism and thermoregulation in common and thick-billed murre. *J. Comp. Physiol. A* 163:160–166.
- De Leeuw J.J. 1996. Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in tufted ducks. *Can. J. Zool.* 74:2131–2142.
- . 1997. *Demanding Divers: Ecological Energetics of Food Exploitation by Diving Ducks*. PhD diss. University of Groningen.
- De Leeuw J.J. and M.R. van Eerden. 1992. Size selection in diving tufted ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. *Ardea* 80:353–362.
- De Vries J. and M.R. van Eerden. 1995. Thermal conductance in aquatic birds in relation to the degree of water contact, body mass and body fat: energetic implications of living in a strong cooling environment. *Physiol. Zool.* 68:1143–1163.
- Handrich Y., R.M. Bevan, J.-B. Charrassin, P.J. Butler, K. Pütz, A.J. Woakes, J. Lage, and Y. Le Maho. 1997. Hypothermia in foraging king penguins. *Nature* 388:64–67.
- Hart J.S. 1951. Calorimetric determination of average body temperature of small mammals and its variation with environmental conditions. *Can. J. Zool.* 29:224–233.
- Hawkins P.A.J., P.J. Butler, A.J. Woakes, and G.W. Gabrielsen. 1997. Heat increment of feeding in Brunnich's guillemot *Uria lomvia*. *J. Exp. Biol.* 200:1757–1763.
- Jenssen B.M. and M. Ekker. 1989. Thermoregulatory adaptations to cold in winter-acclimatized long-tailed ducks *Clangula hyemalis*. Pp. 147–152 in C. Bech and R.E. Reinertsen, eds. *Physiology of Cold Adaptations in Birds*. Plenum, New York.
- Jenssen B.M., M. Ekker, and C. Bech. 1989. Thermoregulation in winter-acclimatized common eiders *Somateria mollissima* in air and water. *Can. J. Zool.* 67:669–673.
- Kleiber M. 1961. *The Fire of Life*. Wiley, New York.
- Kooyman G.L., R.L. Gentry, W.P. Bergman, and H.T. Hammel. 1976. Heat loss in penguins during immersion and compression. *Comp. Biochem. Physiol.* 54A:75–80.
- Kooyman G.L., E.A. Wahrenbrock, M.A. Castellini, R.W. Davis, and E.E. Sinnett. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol. A* 138:335–346.
- Lovvorn J.R. and D.R. Jones. 1991. Effects of body size, body fat, and changes in pressure with depth on buoyancy and costs of diving in ducks *Aythya* spp. *Can. J. Zool.* 69:2879–2887.
- MacArthur R.A. 1984. Aquatic thermoregulation in the muskrat *Ondatra zibethicus*: energy demands of swimming and diving. *Can. J. Zool.* 62:241–248.
- MacArthur R.A. and K.L. Campbell. 1994. Heat increment of feeding and its thermoregulatory benefit in the muskrat *Ondatra zibethicus*. *J. Comp. Physiol. A* 164:141–146.
- McNab B.K. 1980. On estimating thermal conductance in endotherms. *Physiol. Zool.* 53:145–156.
- Michot T.C., A.B. Moser, and W. Norling. 1993. Effects of weather and tides on feeding and flock positions of wintering redheads in the Chandeleur Sound, Louisiana. *Hydrobiology* 279/280:263–278.
- Nehls G. 1995. *Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente Somateria mollissima*. PhD diss. Christian-Albrechts Universität, Kiel.
- Nilsson L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. *Ornis Scand.* 3:55–78.
- Paladino F.V. and J.R. King. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion in white-crowned sparrows *Zonotrichia leucophrys*. *Physiol. Zool.* 57:226–236.
- Pedroli J.-C. 1982. Activity and time budget of tufted ducks on Swiss lakes during winter. *Wildfowl* 33:105–112.
- Pohl H. and G.C. West. 1973. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the common redpoll. *Comp. Biochem. Physiol.* 45A:851–867.
- Prinzinger R., A. Pressmar, and E. Schleucher. 1991. Body temperature in birds. *Comp. Biochem. Physiol.* 99A:499–506.
- Schmidt-Nielsen K. 1975. *Animal Physiology*. Cambridge University Press, Cambridge.
- Stahel C.D. and S.C. Nicol. 1982. Temperature regulation in the little penguin *Eudyptula minor* in air and water. *J. Comp. Physiol. A* 148:93–100.
- Stephenson R. 1994. Diving energetics in lesser scaup *Aythya affinis* Eyton. *J. Exp. Biol.* 190:155–178.
- Stephenson R., P.J. Butler, and A.J. Woakes. 1986. Diving behaviour and heart rate in tufted ducks *Aythya fuligula*. *J. Exp. Biol.* 126:341–359.
- Suter W. 1982. *Vergleichende Nahrungsökologie von überwint-*

- ernden Tauchenten *Bucephala*, *Aythya* und Blässhuhn *Fulica atra* am Untersee-Ende/Hochrhein (Bodensee). Ornithol. Beob. 79:225–254.
- Webster M.D. and W.W. Weathers. 1990. Heat produced as a by-product of foraging activity contributes to thermoregulation by verdins *Auriparus flaviceps*. Physiol. Zool. 63:777–794.
- Wiersma P., T. Piersma, and M.R. van Eerden. 1995. Food intake of great crested grebes *Podiceps cristatus* wintering in cold water as a function of various cost factors. Ardea 83:339–350.
- Wieser W. 1989. Energy allocation by addition and by compensation: an old principle revisited. Pp. 98–105 in W. Wieser and E. Graiger, eds. Energy Transformations in Cells and Organisms. Thieme, New York.
- Wilson R.P. and B.M. Culik. 1991. The cost of a hot meal: facultative specific dynamic action may ensure temperature homeostasis in post-ingestive endotherms. Comp. Biochem. Physiol. 100A:151–154.
- Wilson R.P., K. Hustler, P.G. Ryan, A.E. Burger, and C.E. Nöldeke. 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? Am. Nat. 140:179–200.
- Woakes A.J. and P.J. Butler. 1983. Swimming and diving in tufted ducks *Aythya fuligula* with particular reference to heart rate and gas exchange. J. Exp. Biol. 107:311–329.
- Zerba E. and G.E. Walsberg. 1992. Exercise generated heat contributes to thermoregulation by Gambel's quail in the cold. J. Exp. Biol. 171:409–422.